

A NEW SPECIES OF SPINY-TAILED GECKO (SQUAMATA: DIPLODACTYLIDAE:
STROPHURUS) FROM INLAND QUEENSLAND

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A Spiny-tailed gecko, *Strophurus krisalys* sp. nov., is described from inland areas of Queensland and coastal and near coastal areas in the Gulf of Carpentaria. It has blue mouth colour, enlarged spines above the eye, and parallel rows of enlarged, and uniformly coloured tail spines. In these characteristics it is most similar in morphology to *Strophurus wellingtonae* from inland areas of southern Western Australia, but genetically most similar to the eastern Australian *Strophurus williamsi*. In the north and southeast margins of its range *Strophurus krisalys* is parapatric in distribution with two morphologically different populations of *Strophurus ciliaris*. The new species is arboreal so clearing of native woody vegetation is likely to result in loss and overall fragmentation of populations. □ *Strophurus*, *Gekkonidae*, *Queensland*, *spiny-tail*, *gecko*.

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Strophurus is a morphologically diverse lineage of Australian geckos diagnosed primarily by a character previously considered unique within reptiles: tail glands which produce a viscous substance that is extruded through small rupture sites located on the dorsal surface of the tail (Greer, 1989). Extrusion of glandular secretions from the tail has been reported in the New Caledonian gecko *Eurydactylodes* (Böhme & Sering, 1997), but the mechanism is structurally different and independently evolved.

Greer (1989) identified a small monophyletic species group within *Strophurus* on the basis of small size and lack of femoral pores. The remaining species he regarded as highly divergent in morphology, particularly in scalation, with varying patterns of enlargement of the ciliary, dorsal, and tail scales, forming elongate spines in the most extreme cases. Molecular studies (Melville et al., 2004) identified these as a monophyletic group containing several discrete clades.

Kluge (1967) reviewed the status of *S. ciliaris* (as *Diplodactylus ciliaris*), identifying eight discrete and largely allopatric forms distributed through inland and northern Australia. Kluge identified five populations of *S. ciliaris* with unicoloured tail spines: 'population 3' from southern NT and northern SA; 'population 4' from central northern SA; 'population 6' from inland central Qld; 'population 7' from southwest

Qld; and 'population 8' from inland southern WA. Kluge did not record the species from NSW, although it has since been reported from the northwest of the state (Swan et al., 2004), and the NSW material agrees with Kluge's 'population 7' (pers. obs.), and closes the gap between the Qld material referable to 'population 7' and Kluge's 'population 4' in northeast SA.

Storr (1988) reviewed *D. ciliaris* in WA and recognised three of Kluge's 'populations' and a putative hybrid zone in the west of the continent as species and subspecies: 'population 8' was described as *Diplodactylus wellingtonae*; the hybrid zone between 'population 5' and *S. intermedius* as *D. assimilis*; and 'population 1' and 'population 5' as *D. ciliaris ciliaris* and *D. ciliaris aberrans* respectively.

The status of *S. ciliaris* outside of WA has not been reviewed since Kluge (1967). We focus on the population of *Strophurus* formerly identified as 'population 6' (Kluge, 1967) from Qld using both morphological and genetic data, and described here as *S. krisalys* sp. nov.

MATERIALS AND METHODS

Specimen abbreviations: Specimen abbreviations are prefixed as follows: Australian Museum, Sydney (AMS); Queensland Museum, Brisbane (QM); Western Australian Museum, Perth (WAM); South Australian Museum, Adelaide (SAM); and Northern Territory Museum, Darwin (NTM).

MORPHOLOGICAL ANALYSIS. The main diagnostic characters used are features of tail scalation, and the description and table are based on individuals with complete tails that could be scored for these characters. On these specimens the morphological characters listed below were scored where possible (bilateral scalation characters were scored on both sides and the mean value used).

Measurements: snout to vent length (SVL) - tip of snout to anterior margin of vent; head length - tip of snout to posterior extreme of lower jaw, expressed as a percentage of snout to vent length; head width - width of jaw measured at labials below mid-orbit, expressed as a percentage of head length; snout length - tip of snout to anterior edge of orbit, expressed as a percentage of head length; hindlimb length - groin from apex of crease to tip of fourth toe, excluding claw, expressed as a percentage of snout to vent length; tail length - measured from posterior margin of vent to tip of tail, on complete original tails only, expressed as a percentage of snout to vent length.

Scalation: rostral crease - mid-dorsal groove either partially or completely dividing rostral scale (enlarged scale covering tip of snout), length of groove relative to total height of rostral scale; nasal - number of enlarged scales separating rostral from anterior margin of nostril; supranasal - number of enlarged scales bordering superior margin of nostril; postnasal - number of scales bordering posterior margin of nostril; internasal - number of scales between right and left anterior nasals, immediately posterior to rostral; upper labials - number of enlarged scales bordering upper margin of lip, from rostral to immediately below mid-orbital level; snout scales - number of scales in a longitudinal row from centre of skull at mid-orbit to (and including) scale adjacent to rostral (internasal); interorbitals - number of scales in transverse row across the skull between enlarged ciliaries at mid-orbit; supraciliary - number of enlarged spinose scales projecting beyond margin of dorsal eyelid at its posterior margin; apical plates - the enlarged scales covering terminal underside of digit; fourth finger and toe lamellae - number of scales comprising much enlarged transverse scales on underside of digits (Kluge's secondaries) proximal to apical plates, and number of elliptical or round scales (in pairs) proximal to enlarged transverse scales to emergence of digit (Kluge's tertiaries); tail spines - number of enlarged scales on dorsal surface of tail in regular longitudinal rows, counted from posterior extreme of cloacal swelling to tip of tail; intercaudals - number of scales in a transverse line across tail between

longitudinal rows of caudal spines, counts taken at mid-tail length at row posterior to that bordering anterior edge of caudal spine; outercaudals - number of scales in a transverse line across the underside of the tail between longitudinal rows of caudal spines, counts taken at mid-tail length at row posterior to that bordering anterior edge of caudal spine; intracaudals - number of scales between (but not including the caudal spines of same longitudinal row, counts taken from caudal spine at mid-tail length to next spine immediately posterior; preanal pores - external openings of preanal glands in scales anterior to the vent, and are given as separate values for the left and right sides, counts are for males only; interpore scale - number of scales interrupting the preanal pore series on midline.

DNA EXTRACTION AND SEQUENCING. Samples of those taxa identified as being morphologically similar to the new species were (*S. ciliaris* 'population 7' and *S. wellingtonae*) were included in the genetic analysis using mitochondrial DNA sequences. This comparison was extended to include other populations currently included under *S. ciliaris*, and species from adjacent regions (*Strophurus williamsi*) that might have affinities with, or be confused with, the new species. An individual of *Oedura tryoni* was selected as the outgroup for other diplodactyline taxa.

DNA was extracted from frozen or ethanol-fixed tissue samples using a modified protocol of Saghai-Marooof et al. 1984). About 0.2g of tissue was placed in 600 μ L 2 \times C-TAB buffer (100mM Tris; 1.4M NaCl; 20mM EDTA; 2% hexadecyltrimethylammonium bromide (C-TAB); and 2% 2- β -mercaptoethanol). For all samples, 20 μ L of Proteinase K (20mg/mL) (Amresco) was added and the samples homogenised in microfuge tubes with a plastic pestle. After an overnight incubation at 37°C or two to three hours at 65°C, one volume of phenol:chloroform:isoamyl alcohol (24:24:1 v/v/v) (Sigma) was added, the tubes mixed by inversion and centrifuged at maximum speed for two minutes in an Eppendorf 5154D microfuge. The upper aqueous layer was removed to a fresh tube containing one volume of chloroform:isoamyl alcohol (24:1 v/v) (Amresco). The tubes were again mixed by inversion and centrifuged for two minutes at maximum speed. The aqueous layer was then removed to a fresh tube containing one volume of isopropanol. The tubes were inverted several times and stored

overnight at -20°C . After centrifuging for thirty minutes at maximum speed, the supernatant was removed and $500\mu\text{L}$ of 70% ethanol added to wash the DNA pellet. After brief vortexing, and a final spin for ten minutes at maximum speed, the supernatant was removed and the pellet dried under vacuum for five minutes. Depending on the size of the pellet, gauged by visual inspection, the DNA was resuspended in $100\mu\text{L}$ TE (0.1M Tris, 0.01M EDTA). The amount and quality of DNA was estimated by agarose gel electrophoresis (Sambrook et al., 1989)

Partial sequences of the protein encoding mitochondrial gene for Cytochrome *b* (cyt *b*) and partial sequences for mitochondrial 12S and 16S rDNA genes were obtained. Primer pairs L14841 and H15149 (Kocher et al., 1989) amplified a 307bp fragment of cyt *b*, excluding the primer sequences. The primer pairs L1091 and H1478 (Kocher et al., 1989) amplified a 361bp fragment of the 12S rDNA gene. The primer pairs 16SLF: 5'- CGC CTG TTT ATC AAA AAC AT -3' and 16SHR: 5'- CCG GTC TGA ACT CAG ATC ACG T-3' (H. Lui, pers. comm.) amplified a 507bp fragment of the 16S rDNA gene.

Polymerase chain reaction (PCR) conditions were the same for all primer sets. Amplifications were carried out in $25\mu\text{L}$ volumes containing 1.5 mM MgCl_2 , 0.025mM of each dNTP, 12.5pmol of each primer, 0.2U of Qiagen *Taq* DNA polymerase, $2.5\mu\text{L}$ of Qiagen 10 \times PCR buffer and 1 – 100ng of whole genomic DNA (generally a 1:20 – 1:50 dilution of the stock DNA extraction). A negative control (containing no template DNA) was included for each batch of amplifications. The following cycling profile was used for all experiments: an initial denaturation at 94°C for one minute, then 30 cycles of 94°C for 20 secs, annealing for 30 secs (50°C for cyt *b* and 52°C for 12S and 16S rDNA genes), extension at 72°C for 1½ minutes, and a final extension at 72°C for 2 mins. PCRs were checked for success by running $5\mu\text{L}$ of the reaction on a 2% agarose gel.

PCRs were purified using QIAquick spin columns (Qiagen). Both forward and reverse strands were sequenced using ¼ volume BigDye version 3 Dye Terminator premix (ABI) with the same primers used for the PCR, according to the manufacturer's instructions. The samples were run on an ABI 310 Genetic Analyser. Forward and reverse strands were combined and sequences checked for errors using the computer program Sequencher (Genecodes). Each cyt *b* sequence was examined to establish the absence

of stop codons (the presence of which would indicate a pseudogene or nuclear copy); regions of uncertain alignment of ribosomal genes were excluded from the analysis.

Each gene was aligned first with the computer package ClustalW (Thompson et al., 1994) and then combined and adjusted manually with the Se-Al computer package (Rambaut, 2002). The final alignment consisted of 1185 bases. Regions of ambiguous alignment in the ribosomal DNA genes were excluded. To test for incongruence of phylogenetic signal between the three genes, an ILD test (Farris et al., 1994) was performed in the test version 4.0b10 of PAUP* (Swofford, 2000) therein implemented as a Partition Homogeneity Test.

Genetic distances were calculated using the computer program MEGA version 3.0 (Kumar et al., 2004). The log-determinant (LogDet) distance measure of (Steel 1993) was used, which allows for heterogeneous rates among lineages. Trees were constructed with PAUP* using distance (minimum evolution, ME), maximum parsimony (MP) and maximum likelihood (ML) as the optimality criterion. In each case, the shortest tree was found using a heuristic search with 50 replicates of random taxon addition so as to avoid the tree search being constrained to locally optimum topologies. In most cases, the shortest tree was found after 35 or fewer replicates. For the ME analysis, LogDet distances were used. MP analyses were conducted using the ACCTRAN character optimisation, MULPARS and TBR branch swapping options in PAUP*, as were ML analyses except NNI branch swapping was used. The software program ModelTest v 3.06 (Posada & Crandall, 1998) was used to select parameters of a TnR+ Γ +I likelihood model. Gaps and uncertainties were treated as missing data and all positions were of equal weight. Branch support was assessed for both ME and MP trees with 1000 bootstrap pseudoreplicates (Felsenstein, 1985). For calculation of bootstrap proportions, heuristic searches were carried out as above, but with 35 random addition replicates. ML bootstrap proportions were calculated over 100 pseudoreplicates, with 3 random taxon addition replicates.

The sequences from this study are available on GenBank under accession numbers AY583930-AY583957 for cyt *b*, AY583856-AY583883 for 12S rDNA and AY583903-AY583929 for 16S rDNA.

Table 1. Comparative table of key body measurements and tail scalation for *Strophurus krisalys* sp. nov., *S. wellingtonae*, and *S. ciliaris* 'population 7' from NSW and Qld.

	<i>S. krisalys</i> sp. nov.	<i>S.</i> <i>wellingtonae</i>	<i>S. ciliaris</i> 'population 7'
Maximum SVL(mm)	70.0	82.0	77.0
Tail length (%SVL)			
Range	58.6 – 75.9	64.1 – 79.4	59.7 – 72.3
Mean	66.8	72.0	66.8 ± 0.4
N	28	15	18
Caudal spines			
Range	18 – 21	18 – 22	16 – 22
Mean	19.4 ± 0.8	20.25 ± 1.5	19.1 ± 1.2
N	21	16	14
Intercaudal scales			
Range	8 – 13	7 – 11	4 – 7
mean±sd.	9.8 ± 1.3	9.25 ± 1.3	5.4 ± 0.8
N	27	16	19
Outercaudal scales			
Range	17 – 26	21 – 30	21 – 29
mean±sd	21.5 ± 2.1	25.3 ± 2.7	25.05 ± 2.65
N	27	16	19
Intracaudal scales			
Range	5 – 7	5 – 7	4 – 5
mean±sd	6.0 ± 0.5	5.85 ± 0.8	4.6 ± 0.5
N	25	16	19

SYSTEMATICS

MORPHOLOGICAL COMPARISONS. There is no obvious difference in adult size or body proportions between *S. krisalys* sp. nov. and the 'eastern' *S. ciliaris* 'population 7', but overall adult body size is greater in *S. wellingtonae* than in *S. krisalys* sp. nov. (Table 1).

Direct comparisons of scalation of *S. krisalys* sp. nov. were made with *S. wellingtonae*, the only other *Strophurus* with a similar tail morphology (elevated number of intercaudal scales), and with the parapatric population of *S. ciliaris* from western New South Wales and inland southern Queensland referable to Kluge's 'population 7' that also has enlarged unicoloured spines on the tail. Differences in several scalation characters were observed between *S. krisalys* and *S. wellingtonae* and *S. ciliaris* 'population 7'. In *S. krisalys* sp. nov. (and *S. ciliaris* 'population 7') the enlarged dorsal tubercles are arranged in two parallel but broken rows on each side of the dorsal mid-line of the body, but are present as only a single row on each side of the dorsal

mid-line of the body in *S. wellingtonae*. In *S. krisalys* sp. nov. the longitudinal rows of caudal spines are more widely spaced than in *S. ciliaris* 'population 7', the latter having fewer (almost half the number) of intercaudal scales between the longitudinal rows of caudal spines. There is also a tendency for the rostral groove to be complete in most *S. ciliaris* 'population 7' and *S. wellingtonae*, whereas it is incomplete over a third or more the height of the rostral in *S. krisalys* sp. nov..

For those other populations of *S. ciliaris* with unicoloured tail spines Kluge (1967) gave counts for the number of intercaudal scales that clearly diagnosed those populations as having a much lower number of intercaudals ('population 3' 4-5; 'population 4' 3-5) than *S. krisalys* sp. nov. (8-13). The remaining populations of *S. ciliaris* identified by Kluge, including the nominate population (Kluge's 'population 1'), have a mixture of light and dark coloured caudal spines of varying size, readily distinguishing these populations of *S. ciliaris* from *S. krisalys* sp. nov.

MITOCHONDRIAL DNA. The final alignment consisted of 1185 bases: 507 16S, 371 12S and 307 cyt *b*. Three regions of uncertain alignment in the 16S sequence were excluded from phylogenetic analyses (positions 221-256, 318-320 and 375-377 inclusive). Of the remaining nucleotides, 883 were invariant and 202 were parsimony informative. Twelve equally parsimonious trees were recovered, differing only in the branching order within the *S. ciliaris aberrens* clade. Hierarchical likelihood ratio tests using MODEL TEST suggested the use of a TnR+Γ+I model with the following parameters: base frequencies A=0.3421, C=0.2712, G=0.1566, T=0.2301; substitution rates A↔C=1, A↔G=10.3119, A↔T=1, C↔G=1, C↔T=13.0334, G↔T=1; gamma shape parameter (α) = 0.1815; and proportion of invariant sites = 0.2532. A single ML tree was found (-lnL=3960.44)

Results from the ILD test indicated that there was no significant incongruence between the three datasets (p=0.07, α=0.1), although the 16S dataset produced polytomies in the distal nodes of the tree. In all analyses of the combined data set (ME, MP & ML), each species was recovered as a monophyletic clade with high bootstrap support (most 100%, with *S. ciliaris* ranging from 92% in the MP analysis (Fig. 1) to 96% in the ME analysis). The combined analysis of all three genes clearly identified *S. krisalys* as a

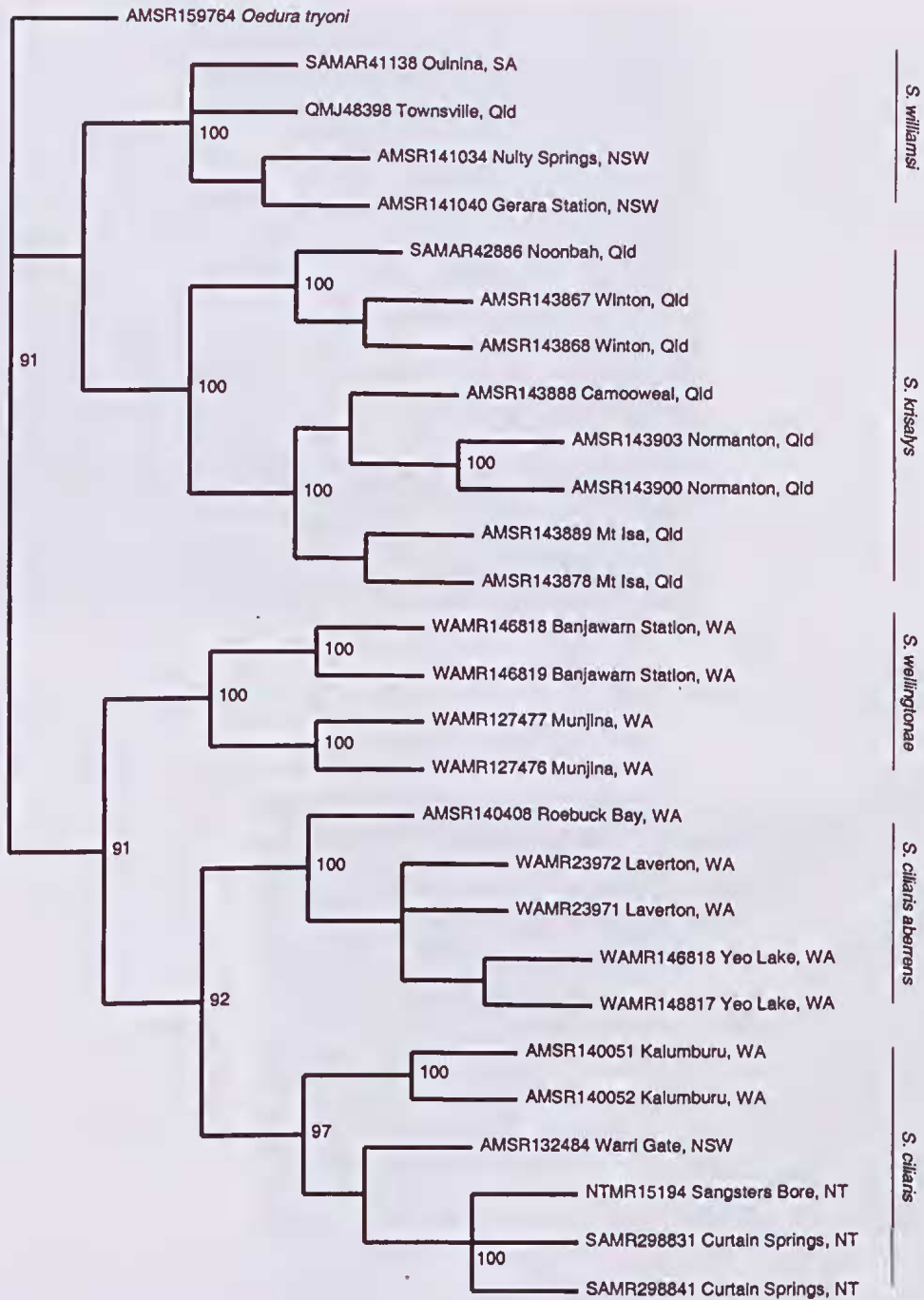


FIG. 1. Maximum parsimony tree of the combined 16S (507 bases), 12S (371 bases) and Cyt b (307 bases) alignment (total length 1185 bases). Bootstrap support was calculated from 1000 replicates of heuristic searches (35 random taxon addition replicates) and is indicated at nodes with values greater than 90%. Maximum likelihood and distance based methods produced similar trees, differing only in the arrangement of individuals from the northern *S. krisalys* sp. nov. population.

distinct group closer to *S. williamsi* than to *S. wellingtonae* or *S. ciliaris*, though bootstrap support for this relationship is unremarkable. Between analyses, the sole topological difference is found between the three northern populations of *S. krisalys*, where the arrangement of individuals is only partially resolved in the ML and ME trees, though bootstrap support varies across all trees (not shown).

Amongst the in-group species, the net distances (Table 2) range from: 0.065 between *S. ciliaris* and *S. wellingtonae*; 0.097 between *S. krisalys* sp. nov. and *S. williamsi*; and 0.109 between *S. krisalys* sp. nov. and *S. wellingtonae*. Within *S. ciliaris*, the subspecies *aberrans* is separated from other *ciliaris* by an average net LogDet distance of 0.053. Within *S. krisalys* sp. nov. a southern group (Noombah and Winton) and a northern group (Mt Isa, Camooweal, and Normanton) separated by a net LogDet distance of 0.044 was found in the combined analysis.

Melville *et al.* (2004) and O'Meally (2004) examined the phylogenetic relationships of *Strophurus*, including *S. williamsi*, *S. wellingtonae* and *S. ciliaris*, among others. In these studies *S. wellingtonae* is a member of the clade that includes *S. ciliaris* and *S. ciliaris aberrans*, and *Strophurus williamsi* a member of a clade that is sister to *S. intermedius*, *S. rankini* and *S. spinigerus*. O'Meally (2004) identified the

TAXONOMIC CONCLUSIONS. It is clear from the genetic data that Kluge's *S. ciliaris* 'population 6' is not conspecific with *S. ciliaris* sensu stricto but closer to the geographically close *S. williamsi*. It is both morphologically and genetically distinct from *S. ciliaris ciliaris* and from *S. ciliaris* 'population 7', which are the geographically closest populations of *S. ciliaris*; from *S. wellingtonae*, which it most closely resembles morphologically; and from *S. williamsi*. Hence, it is described here as a new species:

***Strophurus krisalys* sp. nov.**
(Figs 2, 3)

MATERIAL EXAMINED. HOLOTYPE. QMJ82269 (formerly AMSR143890) 15.6km W of Leichhardt River crossing at Mt Isa on Barkly Hwy, 20°35'S 139°28'E. PARATYPES: *Longreach & Winton District* – AMSR143866-68, QMJ82274-75, 22°19'S 142°43'E. *Mt Isa & Camooweal District* – AMSR143875, on Boulia road, 20°52'S 139°27'E; AMSR143876-77, on Boulia road, 20°45'S 139°29'E; AMSR143878, on Boulia road, 20°44'S 139°29'E; AMSR143879, on Boulia road, 20°44'S 139°29'E; AMSR143883, on Barkly Hwy, 20°00'S 138°34'E; AMSR143889, on Barkly Hwy, 20°26'S 139°24'E; AMSR143884-85, R143888, QMJ82270-71 on Barkly Hwy, 19°57'S 138°25'E; QMJ71634-35 on Boulia road, 20°45'S 139°29'E. *Normanton & Croydon District* – AMSR63394 Normanton, 17°42'S 141°04'E; AMSR63482-84 Normanton, 17°40'S 141°04'E; AMSR63512-5 Normanton, 17°40'S 141°04'E; AMSR63573, Normanton 17°40'S 141°04'E; QMJ82272, Normanton, 17°41'S 141°03'E; AMSR143900 Normanton, 17°42'S 141°02'E; QMJ82273, Normanton, 17°44'S 141°02'E; AMSR143908 Normanton, 17°47'S 141°00'E; AMSR143902 Normanton, 17°48'S 141°00'E; AMSR143903 Normanton, 17°50'S 140°59'E; AMSR143904, Normanton, 17°51'S 140°58'E; AMSR143906 Normanton, 17°52'S 140°57'E.

TABLE 2: Net genetic distances (LogDet) between species included in the mitochondrial DNA analysis.

	1	2	3	4	4a	4b	6
<i>S. krisalys</i> sp. nov. (1)	-						
<i>S. williamsi</i> (2)	0.097	-					
<i>S. wellingtonae</i> (3)	0.109	0.088	-				
<i>S. ciliaris</i> all samples (4)	0.080	0.088	0.065	-			
<i>S. ciliaris aberrans</i> (4a)	0.125	0.110	0.087	-	-		
<i>S. ciliaris</i> (4b)	0.114	0.097	0.074	-	0.053	-	
<i>O. tryoni</i> (6)	0.167	0.154	0.159	0.142	0.158	0.154	-

sister relationship of *S. williamsi* and *S. krisalys* sp. nov. Melville *et al.* (2004) reported uncorrected sequence divergences between *S. williamsi* and *S. wellingtonae* of 0.13; *S. ciliaris* of 0.11; and *S. ciliaris aberrans* of 0.11. The topologies and divergences observed are similar to those found in this study and suggest further genetic comparisons of *S. krisalys* sp. nov. with other members of the genus are not warranted.

The type series was chosen from areas represented by specimens used in the genetic study. The registration numbers and corresponding tissue numbers (bracketed) for the specific individuals used in the analyses are as follows: AMSR143866 (NR2365); AMSR143867 (NR2366); AMSR143878 (NR2370); AMSR143888 (NR2458); AMSR143889 (NR2459); AMSR143900 (NR2378); AMSR143903 (NR2377).

DIAGNOSIS. *Strophurus krisalys* can be distinguished from other members of the genus



FIG. 2. *Strophurus krisalys* sp. nov. (AMSR143902) from near Normanton, Qld.

dorsal mid-line of the body (vs a single row each side of the dorsal mid-line of the body), and partially (vs completely) divided rostral scale.

It is distinguished from the genetically closest species *S. williamsi* by having a single (vs double) row of enlarged, unicolored, spinose, tubercles on either side of the tail.

ETYMOLOGY. For Kristin Alys Sadlier (*krisalys*).

DESCRIPTION. *Measurements*: SVL and Tail length given in Table 1; head length 22.1-25.9% of body length (=24.0%, n=29); head width 60.0-72.5% of head length (=65.6%, n=

(as defined by Greer, 1989) by its moderately large size, maximum snout to vent length 70.0mm; two rows of enlarged tubercles each side of the dorsal mid-line of the body; a single row of enlarged, spinose tubercles on either side of the tail; spinose scales of tail unicoloured; mouth colour deep blue.

Of species likely to be confused with *S. krisalys* only *S. ciliaris* 'population 7' and *S. wellingtonae* have a single row of enlarged, unicolored, spinose, tubercles on either side of the tail. *S. krisalys* can be distinguished from these species as follows: from parapatric *S. ciliaris* 'population 7' by the deep blue (vs yellow) mouth colour and greater number of intercaudal scales (8-13 vs 4-7); from *S. wellingtonae* by two parallel rows of enlarged tubercles each side of the

29); snout length 40.0-45.6% of head length (=42.6%, n = 29).



FIG. 3. *Strophurus krisalys* sp. nov. (AMSR143869) from near Winton, Qld.

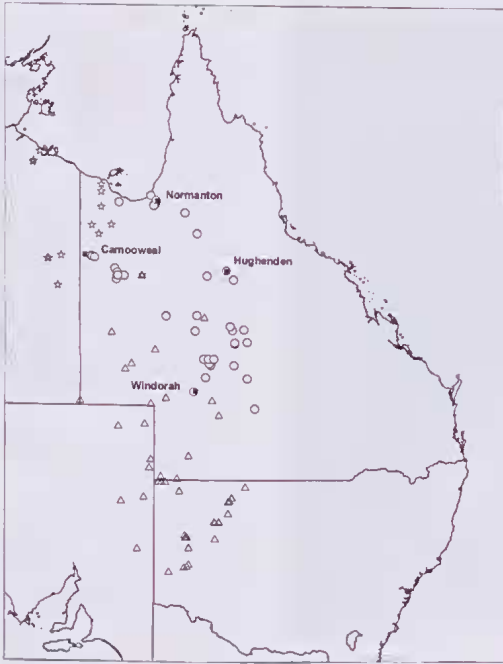


FIG. 4. Distribution map showing museum records for *Strophurus krisalys* sp. nov. (open circle); *S. ciliaris sensu stricto* (open star); and *S. ciliaris* 'population 7' (open triangle).

Scalation: Nostril surrounded by rostral, single supranasal, single postnasal, and first labial. Median groove of rostral up to two thirds height of the scale. Internasals 1-3. Upper labials 8-11 ($= 9.4 \pm 0.7$, $n = 29$). Interorbitals 25-32 ($= 28.6 \pm 1.6$, $n = 26$). Upper margin of eye with 1-3 enlarged ciliary spines, posterodorsal margin 1-2 smaller ciliary spines. Underside of digits of forelimbs with single pair of large apical plates, followed on fourth digit by 4-5 transverse lamellae and proximally by 0-3 pairs of elliptical or circular scales. Underside of digits of hind limbs with pair of large apical plates, followed on fourth digit by 3-5 transverse lamellae and proximally by 0-2 pairs of elliptical or circular scales. Preanal pore row in males discontinuous, 3-7 on left and 4-7 on right side, and separated by up to 4 scales lacking pores.

Dorsal tubercles arranged as two parallel rows each side of the dorsal mid-line of the body, tending to be widely spaced and scattered posteriorly. Enlarged, spinose, tubercles of tail arranged as a longitudinal row of 18-21 ($= 19.4 \pm 0.8$, $n = 21$) spines on either side of the tail, at mid-distance along tail parallel rows are

separated transversely by 8-13 ($= 9.85 \pm 1.3$, $n = 27$) homogenous flat intercaudal scales and 17-26 ($= 21.5 \pm 2.1$, $n = 27$) outercaudal scales, and along each row the spines at mid-distance along tail are separated longitudinally by 5-7 ($= 6.0 \pm 0.5$, $n = 25$) intracaudal scales.

Colour and Pattern. Specimens from the far north of the species range in the Gulf of Carpentaria usually have a vertebral pattern of well-defined and contrasting dark transverse ellipses which contact medially along the vertebral margin (Fig. 2). Some well marked individuals also have a lateral extension of these dark blotches present as hourglass shaped blotches on the side of the body. The dark dorsal pattern is reduced in two specimens; one is nearly uniformly grey. Specimens from further south have a higher proportion of uniformly coloured individuals (Fig. 3) in the samples.

DISTRIBUTION. Inland Queensland from Winton and Ambathala in the south through to Normanton in the north, and west to Camooweal (Fig. 4). It is parapatric in distribution with *S. ciliaris* 'population 7' over much of its distribution in the south and southwest, but both species are recorded in the Winton region and sympatry between the two species could be wider than the available samples indicate. In the north of its distribution it is broadly parapatric with *S. ciliaris sensu stricto*.

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- used in compiling the distribution map (Fig. 4) are also listed.
- Strophurus krisalyss* sp. nov. – additional material examined but not included in type series: QMJ312 Normanton, 17°40'S 141°04'E; AMSR52690-91 Karumba, 17°29'S 140°50'E; QMJ28187 Normanton, 17°40'S 141°04'E; AMSR20800 Burketown, 17°45'S 139°33'E; AMSR63613 8.1km W Croydon P.O., 18°09'S 142°13'E; QMJ47535 Esmeralda 19°00'S 142°44'E; AMSR72045 Camooweal, 19°58'S 138°29'E; QMJ24480 Hughenden, 20°31'S 143°54'E; QMJ39030 Mt Isa, 20°43'S 139°31'E; AMSR15138, R26009, R27331-32, R28417-23, R28443, R28448-49, R50738, R64840 Mt Isa, 20°44'S 139°29'E; QMJ30337 Mt Isa, 20°44'S 139°29'E; QMJ31546 Richmond, 20°44'S 143°08'E; AMSR60284 Cloncurry, 20°44'S 139°47'E; AMSR142963 Middleton, 22°21'S 141°28'E; QMJ49968 Acacia Downs, 22°47'S 144°04'E; QMJ57232 Crossmoon Stn, 22°54'S 144°37'E; QMJ8540 Darrivcen Stn, 22°56'S 144°10'E; QMJ29124 Mt. Cameron Stn, 22°58'S 142°39'E; QMJ9563 Currane, 23°24'S 144°45'E; QMJ15334 Hughenden, 20°51'S 144°12'E; QMJ54614 Longreach, 23°27'S 144°15'E; QMJ58757 Longreach, 23°26'S 144°15'E; QMJ30324, QMJ32589, QMJ37672, Longreach, 23°26'S 144°15'E; QMJ49796 Longreach, 23°26'S 144°15'E; QMJ52596 Noonbah airstrip, 24°05'S 143°01'E; QMJ58758 Noonbah, 24°05'S 143°11'E; SAMR42886¹ (C038) Noonbah; QMJ58759 Tarcombe Reserve, 24°06'S 143°24'E; QMJ9660 Stonehenge, 24°21'S 143°17'E; QMJ56844 Waterloo, 24°16'S 143°13'E; QMJ6241 Ruthven, 24°20'S 144°11'E; QMJ7879 Jundah, 24°50'S 143°04'E; QMJ61083-84 Idalia N.P. 24°52'S 144°46'E; AMSR141929-30 Windorah 25.25'S 142.36'E; QMJ35686, QMJ35703 Ambathala N.R., No. 3 Bore, 26°05'S 145°04'E.
- Strophurus ciliaris aberrans* (WA): WAMR146816¹ (JEM 32), WAMR146817¹ (JEM 25) Yeo Lake Road 29°09'S 123°48'E; WAMR23971¹, WAMR23972¹ Laverton; WAMR140408¹ (NR1894), Broome.
- Strophurus ciliaris ciliaris* (WA): AMSR140051¹ (NR1063), R140052¹ (NR1064) McGowens Beach, 14°09'S 126°38'E;
- Strophurus ciliaris ciliaris* ? (NT): SAMR29883¹ (ABTC 4220 = BM044), SAMR29884¹ (ABTC 4220 = BM045) Curtain Springs; NTMR15194¹ (SQ97) Sangsters Bore.

Appendix

ADDITIONAL MATERIAL EXAMINED: Specimens of *Strophurus krisalyss* sp. nov., *S. ciliaris* 'population 7', and *S. wellingtonae* marked with an asterisk were used in compiling Table 1. Specimens used in the genetic study are marked with a superscript ¹; tissue collection numbers are indicated in brackets. Specimens

Strophurus ciliaris ciliaris (Qld.): QMJ28734, Mornington Is. 16°29'S 139°34'E; QMJ47687 Doomadgee, 17°02'S 138°49'E; QMJ51986 Lawn Hill. 18°42'S 138°28'E; QMJ47683 Doomadgee, 17°19'S 138°49'E; QMJ10727, QMJ10908, QMJ10918 Doomadgee, 17°56'S 138°49'E; QMJ2220 Gregory Downs, 18°39'S 139°15'E; QMJ46853 Riversleigh, 19°02'S 138°45'E; QMJ7536 Cloncurry, 20°42'S 140°30'E; QMJ34805-06 Georgina Downs, 21°08'S 137°04'E.

Strophurus ciliaris 'population 7' (Qld): QMJ7535 Cloncurry, 20°42'S 140°30'E; QMJ34587 Winton, 22°23'S 143°02'E; QMJ43295 Herbert Downs, 23°02'S 139°18'E; QMJ43320-23 Spring Valley, 23°41'S 141°02'E; QMJ48490 Natan Stn, 28°00'S 142°25'E; QMJ58748 (NR2472) Davenport Downs, 24°15'S 140°05"E; AMSR139808* 32.7km SE Thylungra on Damantina Developmental road (Quilpie-Windorah); AMSR139834* Bedourie, 24°27'S 139°49'E; QMJ26476 Quilpie, 25°53'S 143°25'E; AMSR113246* Simpson Desert, 25°46'S 138°00'E; QMJ26475-76, QMJ26511 Cuddapan Stn, 25°39'S 141°30'E; QMJ41760 Beetoota, Wyeroe Ck., Mt. Leonard Stn, 25°52'S 140°53'E; AMSR32601 Omicron, 28°49'S 141°16'E.

Strophurus ciliaris 'population 7' (NSW): AMSR132484*¹ (NR358) Warri Gate, 9.8km N, 28°55'S 141°56'E; AMSR155243, R155396 Sturt National Park, 29°02'S 141°18'E; AMSR155249 Sturt National Park, 29°02'S 141°11'E; AMSR155418 Sturt National Park, 29°01'S 141°27'E; AMSR147602 Thoura, 29°16'S 144°41'E; AMSR90907 Tibooburra, 29°26'S 142°01'E; AMSR130500 Wanaaring, 29°43'S 144°07'E; AMSR130853-54 Wanaaring, 29°42'S 144°09'E; AMSR40456, R40815-6, R41085-86 Goorimpa Station, 30°20'S 144°01'E; AMSR161531-34, R161543-44, R161554, R162658 Paroo-Darling National Park, 30°40'S 143°37'E; AMSR161557 R162587, R162629, R162687, R162715 Paroo-Darling National Park, 30°41'S 143°37'E; AMSR161561, R161639 Paroo-Darling National Park, 30°41'S 143°36'E; AMSR162685 Paroo-Darling National Park, 30°43'S 143°28'E; AMSR162710 Paroo-Darling National Park, 30°41'S 143°27'E; AMSR141904 Coolabah tip, 31°02'S 146°43'E; AMSR150157 Mootwingee National Park, 31°12'S 142°15'E; AMSR146259 Mootwingee National Park, 31°17'S 142°18'E; AMSR146260, R147273 Mootwingee National Park, 31°18'S 142°20'E; AMSR141893

Girilambone tip, 31°15'S 146°54'E; AMSR132985* Wilcannia, 27km - Wanaaring road, 31°22'S 143°28'E; AMSR107243* Menindee caravan park, 32°24'S 142°25'E; AMSR32811 Kinchega National Park, 32°29'S 142°21'E; AMSR121034* Lake Cawndilla, 32°31'S 142°14'E; AMSR138418 S of Broken Hill, 32°43'S 141°36'E; AMSR123947 E of Broken Hill, 31°44'S 142°25'E.

Strophurus ciliaris 'population 7' (SA): SAMR14841 Koonchera Dune, 26°47'S 139°33'E; SAMR16815 within 3km of Strathearn, 31°46'S 140°20'E; SAMR25596 Cordillo Downs Stn., 26°42'S 140°37'E; SAMR38247 6km S of Innamincka Bore No. 3, 28°09'S 140°53'E; SAMR39966 14km SW of Innamincka Bore 2, 28°28'S 140°49'E.

Strophurus wellingtonae (WA): WAMR8963* Austin Downs, 27°23'S 117°45'E; WAMR21112* 34 miles E Wiluna, 26°40'S 120°46'E; WAMR27216* Wanjarri Station, Kathleen Valley, 27°19'S 120°33'E; WAMR81320* 2km S Capricorn Roadhouse, 22°26'S 119°47'E; WAMR65871* 2.5km N Mt Linden, 29°1'S 122°25'E; WAMR87463* 3km E White Well, 26°5'S 120°06'E; WAMR87484-86* 20km E Millbillillie, 26°37'S 120°3'E; WAMR87491* 26km W Prenti Downs homestead, 26°34'S 122°34'E WAM105548* 27km S Leonora, 29°06'S 121°21'E; WAMR104489* 42km W Newman, 23°12'S 119°19'E; WAMR127476¹ (W12) & WAMR127477¹* (W14) Minjina Roadhouse, 22°33'S 118°3'E; WAMR146818¹ (JEM30); WAMR146819¹ (JEM29) Banjawam Station, 27°36'S 121°40'E.

Strophurus williamsi: AMSR141039¹ (NR1292) Nulty Springs, New South Wales; AMSR141040¹ (NR1293) Gerara Station, NSW; QMJ48398¹ (ABTC16229) Townsville, Qld; SAMR41138¹ (ABTC39708) Oulnina SA.